

A STATISTICAL STUDY OF TAXONOMIC CATEGORIES
IN ANTS (FORMICIDAE: LASIUS NEONIGER
AND LASIUS AMERICANUS)¹

ELLA VIRGINIA GREGG

Hull Zoological Laboratory,
University of Chicago

This work is an attempt to analyze statistically the differences which separate two varieties of the ant *Lasius niger*, namely variety *neoniger* Emery and the subspecies *alienus* Förster variety *americanus* Emery. It tests the morphological characters used by taxonomists to separate these forms and correlates the differences with their ecological distribution.

An examination of Talbot's (1934) table of ant distribution in the Chicago area showed two good cases (*Formica pallide-fulva* complex and *Lasius niger* group) of distributional overlap of varieties in certain portions of their ranges. The *Lasius niger* group was chosen for study because of measurable, morphological differences between the workers of the two varieties.

It has long been recognized that ant nomenclature is complicated, employing as it does the quadrinomial system, and that a very real need for simplification exists. While subspecies may be divided into smaller categories that are real on theoretical grounds, the bases for such separation often cannot be subjected to critical evaluation. Creighton (1938) summarizes briefly the history of the system, points out the value of adequate field studies to demonstrate the geographical nature of infra-specific categories, and advocates the merging of the two subspecific ranks. Buren (1944) follows Creighton's lead and recognizes only one infraspecific unit, the subspecies. However, unlike Creighton who believes most subspecies are geographical races, Buren favors the ecological nature of many variants. Cole (1938) would eliminate varieties of species or subspecies because they are ecologically or geographically isolated populations within a species which yet intergrade with the species and are thus actually of subspecific rank. Mayr (1942) points out the frequent occurrence among ants of sibling species most of which are still called subspecies or varieties even though they may live in the same habitat but behave like different species. With additional field work to determine the actual geographic range and ecologic distribution of various forms, simplification of Formicid nomenclature should proceed along two lines: (1) the realization that infraspecific ranks are but steps of greater or lesser magnitude in the speciation process and the possibility then of elimination of the varietal category, and (2) the recognition and elevation to specific rank of morphologically

¹The author wishes to express sincere appreciation to Dr. A. E. Emerson for generous assistance and to Dr. Thomas Park for aid in the statistical analysis. Many thanks are extended to her husband, Dr. R. E. Gregg, and to Dr. Thomas Park for critical readings of this manuscript. Dr. N. A. Weber kindly gave specimens of the European *Lasius niger* for comparison with the American forms studied.

similar races (sibling species) which conform to the modern species concept (see discussion).

The varieties used in the study are two of the new world representatives of the old world species *Lasius niger* L. The European *Lasius niger* has one subspecies pertinent to this discussion, *alienus* F., though Bondroit (1918) and Donisthorpe (1915, 1927) consider it a distinct species. *Lasius niger* workers are darker, have a more pubescent body and are larger in size than *alienus*, and have erect hairs on tibiae and antennal scapes in contrast to lack of hairs on *alienus*. The two forms are similar in geographical distribution, though *niger* appears more widely spread covering probably the whole of the *alienus* range and is commoner in northern Europe (Donisthorpe 1927). Diver (1940) reports interesting ecological differences between *niger* and *alienus* in a survey of the South Haven Peninsula in England which he believes supports their specific distinctness: *niger* has a wide tolerance, occurring in all eight habitat types, while *alienus* is much restricted, 81 per cent of its recorded loci being on dry heath. Interestingly, he reports the dry heath habitats on the Peninsula are partly composed of Eocene Bagshot beds and partly of recent wind blown sand, with *niger* largely confined to the Bagshot heaths and *alienus* to the sand. This suggests that soil structure might be an important isolating factor.

The new world variety *neoniger* was described by Emery (1893) and Wheeler (1905, 1908, 1917) substantiated it. The variety *americanus* was originally described by Emery (1893) as a variety of *Lasius niger* L. and Wheeler (1905, 1908) concurred but later (1917) concluded it should be attached to the European subspecies *alienus* since erect hairs are missing on the legs and antennal scapes and the body is sparsely haired. On the basis of the present analysis, these varieties are raised to specific rank and will be called *Lasius neoniger* Emery and *Lasius americanus* Emery in the subsequent discussion.

TAXONOMIC AND ECOLOGIC LITERATURE

Lasius americanus Emery

Lasius niger (L.) *alienus* Förster var. *americanus* Emery.

Wheeler, W. M. 1917. pp. 525-526, ♀ ♂.

Wheeler, W. M. 1916. p. 463, ♀.

Lasius niger (L.) var. *americanus* Emery.

Emery, C. 1893. p. 639, ♀ ♂.

Wheeler, W. M. 1905. p. 393, ♀.

Wheeler, W. M. 1908. p. 623, ♀.

Lasius niger (L.) var. *alienus* Förster.

Mayr, G. 1886. p. 429.

Lasius alienus Förster.

Provancher, L'Abbe. 1887. p. 236, ♀ ♂.

? *Formica pallitarsis* Provancher.

Provancher, L'Abbe. 1881. pp. 355-356, ♀ ♂.

Formica aliena Förster.

Förster, A. 1850. pp. 36, 71, ♀ ♂.

Lasius americanus is distinguished from *Lasius neoniger* by the absence of suberect hairs on the tibiae and antennal scapes in the female and worker (Wheeler 1916a), and by the sparse pilosity of the body. The workers are rather small averaging about 3 mm. in length (Cole 1940, 1942). Wheeler (1917) records two forms of *americanus* females: the typical eastern form is from 5–5.5 mm. long with wings not exceeding 8 mm. in length; the western form measures nearly 8 mm. with wings 9–10 mm. long. The latter is recorded by Wheeler as indistinguishable in stature from the female of the true European *alienus* and might be regarded as a variety. The males are also stated to vary greatly in size.

This form is the commonest of the numerous species of *Lasius*. It occurs over North America except the extreme southern (found in northern Florida) and southwestern portions, extending from timberline to the seashore. The literature on the ecological range of the variety is contradictory. Talbot (1934), in the Chicago region, found *americanus* nested indifferently under stones, in soil or in logs, and entered the Indiana dune succession only where mesic conditions prevailed. When *americanus* was tested for toleration of dryness against *neoniger*, no real difference was found, though the second experiment showed a borderline significance favoring *americanus*. However, neither variety emerges from the nest during low relative humidity so they do not face severe conditions.

Gregg (1944) in the same region reports *americanus* occurs from dry open pastures to the interior of climax forests and may be found nesting in logs or under sticks or stones or other suitable cover.

Cole (1934) lists *americanus* as a very common occupant of more moist areas throughout Idaho. The same author (1933) considers it the dominant ant in one of three vegetative communities in an area one-tenth of a mile square in sage-brush semi-desert near Twin Falls, Idaho. The community bordered a small stream and the soil was a moist, rich loam.

Wheeler (1908) says *americanus* is common on dry, sunny heaths, and like the European *alienus*, is a hairless or nearly hairless, xerothermic variety of *niger*. Wheeler (1910) states *americanus* is the form usually occurring in higher and drier pastures and fields. In Utah, Cole (1942) reports colonies in the soil beneath stones, particularly in the more open and grassy areas. Some nests were observed at 6500 feet elevation. Cole (1940) mentions its occurrence in dark, forested areas in the Smoky Mountains but also states its colonies are numerous especially in dry, open situations, such as sandy places, grassy fields and slopes, or very open woods. It is found as high as 3800 feet but is more abundant at lower elevations.

Most authors consider the variety well adapted to the diverse physical conditions which it encounters. Headly (1943) finds *americanus* the commonest ant in Ashtabula County of Ohio, occurring in fields or woods and in damp or dry ground. Indifference to nesting site location in an Ohio prairie region was reported by Amstutz (1943) since *americanus* was found in every location and in all types of habitat. Wesson and Wesson (1940) in a south central Ohio collection, list *americanus* as one of the species found nearly everywhere, though more

TABLE I
Dates on Which Sexual Phases of *Lasius neoniger* Emery and *Lasius americanus* Emery Have Been Observed

	<i>Lasius neoniger</i>	<i>Lasius americanus</i>
April		April 19, 1920 M.; Q. April 19, 1920 M.; Q. Lawrence, Kansas (Hayes, 1925) Staten Island, New York (Davis and Bequaert, 1922)
May		May 8, 1937 Q. P. May 29, 1937 Q. P. May 23, 1936 Q. P. Volo, Illinois Lakeside, Michigan Smith, Indiana
June	June 26, 1937 Q. P. Miller, Indiana Summer months Q. Davis, California (Mallis, 1941)	June 21-27 M.; Q. June 29, 1937 M.; Q. Last half June Q.; Q. P. M.; Q. Snake River Plains, Idaho (Cole, 1934) (Earliest appearance date.) (Wheeler, 1905) Smith, Indiana (Low elevations) Great Smoky Mountains, Tennessee (Cole, 1940)
July	July 24, 1937 M. Tremont, Indiana July 24 M.; Q. (Earliest data collected) Cape Cod, Massachusetts (Sturtevant, 1931) Summer months Q. Davis, California (Mallis, 1941)	July M.; Q. (Higher elevations) Great Smoky Mountains, Tennessee (Cole, 1940) July M.; Q. July 11 M.; Q. Snake River Plains, Idaho (Cole, 1934) (Earliest date collected) Cape Cod, Massachusetts (Sturtevant, 1931) July 17, 1937 M. Late July M.; Q. Hodgkins, Illinois (Earliest date collected) Ashtabula County, Ohio (Headley, 1943)
August	August 14, 1932 M.; Q.; S. St. Louis County, Missouri (Rau, 1934) August 28, 1937 M. Monroeville, Illinois Summer months Q. Davis, California (Mallis, 1941)	August M.; Q. August M.; Q. August M.; Q. Snake River Plains, Idaho (Cole, 1934) Connecticut (Wheeler, 1916b) West Point (Smith, 1934b)
September	Sept. 2, 1939 Q. Indian Gap, Great Smoky Mountains, Tennessee (Cole, 1940) Sept. 3 M.; Q. (Latest date collected) Cape Cod, Massa- chusetts (Sturtevant, 1931)	Sept. 14, 1935 M. Sept. 14, 1935 S. Mid-September M.; Q. Sept. 18, 1938 M.; Q. Sept. 19 and 20, 1910 M.; Q.; S. Sept. 9, 18, 20 M.; Q.; S. Sept. 5, 19-29 S. E. Sept. 30 M.; Q. Lawrence, Kansas (Hayes, 1925) Urbana, Illinois (Forbes, 1908) (Latest date collected) Ashtabula County, Ohio (Headley, 1943) Cove Mountain, Great Smoky Mountains, Tennessee (Cole, 1940) Charity Islands, Lake Huron (Gaige, 1914) Illinois (Tanquary, 1913) Illinois (Tanquary, 1913) (Latest date collected) Cape Cod, Massachusetts (Sturtevant, 1931)
October		October 4, 8, 11 S. E. October 1-15 Q. Illinois (Tanquary, 1913) West Point (Smith, 1934b)

Q. = Winged queens Q. P. = Queen pupae M. = Males S. = Swarming S. E. = Swarming evidence (dealtated queens)

abundant in drier and open localities. Yet they also say it is one of the three principal species found in low, moist woods. The great adaptability of *americanus* is evidenced by its nesting habits; it may be found from damp, rotting wood of dense forests to the sandy soil of dry, sunny roads (Burrill and Smith 1919; Dennis 1938; Forbes 1908; Wheeler 1905, 1916b, 1917). Dennis reports *americanus* in every locality collected in Tennessee and also on top of the mountains well over 6000 feet in contrast to Cole's 3800 feet. Gaige (1914) relates that *americanus* is a notoriously ubiquitous species but even it shows habitat preferences. Thus out of seven ant habitats listed for the largest of the Charity Islands, situated at the mouth of Saginaw Bay in Lake Huron, *americanus* occurs in five: low hardwood forest, high hardwood forest, open woodland, willow and dogwood thickets, and grassy beach areas. Of the last, Gaige reports the form "apparently prefers this habitat." This is of particular interest since the community as described is somewhat the same as the Indiana-Michigan dunes where extensive collecting was done for this study, and *americanus* was never found along the beach areas. Except for rocky shores, the island Gaige examined was composed of old dunes of varying size and was entirely covered with original forest.

The color of *americanus* workers (Cole 1940, 1942) varies from light to dark brown. Wheeler (1905, 1916b, 1917) and Cole (1940) report the workers of colonies living in dry, sunny areas are much paler in color than the woodland inhabitants, and Wheeler (1905) believes the paler forms might be regarded as representing a different variety. Sturtevant (1931, p. 76) indicates what he considers to be two types on Cape Cod. "There appear to be two distinct forms here—a darker form typically nesting in stumps and logs in the woods, not found infested with Mermithids; and a paler form typically nesting in the soil in sunny places (often on the beaches down to high-tide level, frequently producing short-winged mermithogynes [Mermis parasitized winged females]) . . . In the absence of adequate series from the Palaearctic region and from the western states, I am unable to make a thorough revision of the forms of *niger*—without which it seems to me undesirable to describe and name these types." Sturtevant probably is dealing either with color variants of *americanus* or he may have both *americanus* and *neoniger*. Wheeler (1908, p. 623) states that *americanus*, when nesting in shady woods or damp spots, "usually has a darker color and may develop a few erect hairs on the scape and legs, thus approaching the smaller and darker forms of *neoniger*."

These intermediate forms suggest the possibility of hybridization. The literature contains scattered information on swarming dates and dates on which winged forms have been collected in the nests. Table I presents these data.² *Americanus* appears to have reproductives in the colony for a longer period of the year than does *neoniger*, but this may only be due to the larger number of *americanus* records available. In addition to the data in Table I, Tanquary (1913) states that nuptial flights of *americanus* usually occur from August to September, and

²Since this paper went to press, Talbot (1945) has published additional swarming dates for *Lasius americanus* at Tiffin, Ohio, as well as valuable swarming behavior data. The swarming dates are August 30, 31, and September 4, 15, 28 in 1943.

Turner (1915) describes a swarming flight of *Lasius niger* L. on September 17, 1913, but the variety is not given. Since the nests were common in St. Louis, Missouri, and the swarm observed was in Turner's yard, he is referring presumably to *neoniger*. Smith (1934b) places *neoniger* among the species that usually do not produce sexual phases until late in the season. Gaige (1914) reports a *neoniger* swarm on the Charity Islands four days prior to an *americanus* swarm; the latter apparently refers to the *americanus* mating exodus of September 19 and 20, 1910, listed in Table I. Thus the swarming periods for the two forms do overlap and while the mating flights probably do not occur at the same time in any given locality, and ecologically the species are largely distinct, it is not possible to rule out the phenomenon of hybridization as crossing might occasionally take place. Such infrequent matings would not invalidate the specific status of the forms (species definition under later discussion).

***Lasius neoniger* Emery**

Lasius niger (L.) var. *neoniger* Emery.

- Emery, C. 1893. p. 639, ♀.
 Wheeler, W. M. 1905. p. 396.
 Wheeler, W. M. 1908. p. 622, ♀ ♀.
 Wheeler, W. M. 1917. p. 525, ♀ ♀ ♂.

Lasius niger (L.):

- Mayr, G. 1886. p. 429.

The worker body length of *Lasius neoniger* is given by Cole (1940) as about the same as *americanus* (3 mm.), but Wheeler (1917) describes the worker and male length as only 2–2.5 mm. The female of *neoniger* is 6–7 mm., the wing length is 8–9 mm., and in both the male and female are hyaline (Wheeler 1917). Yet Wheeler (1908) states the female of *neoniger* is much larger than *americanus*, being 9–10 mm. long and with wings 9–9.5 mm. in length and tinged with yellow.

This form occurs over most of the United States though it does not extend as far south as *americanus* and is much less abundant. Smith (1927, 1934a) reports *neoniger* in South Carolina and also in Mississippi but it is subboreal (Cole 1942; Wheeler 1904, 1905, 1916a, 1917), and some of its southern distribution may be due to the altitude at which it is found (Dennis 1938; Cole 1940, Wheeler 1904). *Neoniger* is reported by Gregg (1944) to replace *americanus* in pioneer Indiana dune stages. Talbot (1934) found *neoniger* craters abundant in the early stages of the Indiana dune succession and records it as one of the two characteristic ants in the foredune and poplar associates. Also it occurs in the pine dunes and in the open sand areas in the black oak dunes. Apparently herbaceous vegetation quickly eliminates it, and the lack of an open substratum appears to be a limiting factor in this case. As stated before, Talbot found no positive evidence of differential response to dryness between the two species.

The literature on its ecological range is fairly consistent. Wheeler (1908) states that *neoniger* is found only in moist localities, especially in sunny, subalpine meadows. The usual niche for this form seems to be in the soil, beneath stones or logs in rather open forests, borders of

woods, clearings, grassy areas, or even in city parks and gardens (Cole 1940; Dennis 1938; Headley 1943; Morris 1943; Wheeler 1905). Gaige (1914) states *neoniger* is restricted to the grassy beach habitat on the largest of the Charity Islands. Headley (1943) affirms the variety has a "preference" for sandy soil, and replaces in abundance *americanus* in this habitat.

The color of *neoniger* workers varies from pale to dark brown (Cole 1940). Sturtevant (1931) believes that in the Cape Cod region of Massachusetts, *neoniger* is not clearly distinct from *americanus* and he identifies all the intermediates as *americanus*. He suspects the extreme hairy specimens are not really distinct from the paler *americanus* forms he refers to (see quotation under *Lasius americanus*). It is also interesting to note that Wheeler (1908, p. 622) states under *neoniger*: "Smaller, darker forms, with less pubescence and forming transitions to some of the subvarieties of var. *americanus* Emery and the European *alienus* Först. occur in many localities throughout the Northern States." The meaning of "subvariety" is not clear. It is pertinent here to recall the earlier discussion of swarming dates and the suggestion of hybridization between the species.

COLLECTION TECHNIQUE

Collections for this study were made within a ninety mile radius of Chicago, and the major habitats in the area were thoroughly covered. It is hardly necessary to redescribe the plant communities listed in Table II as Cowles (1901), Fuller (1925), Talbot (1934), and R. E. Gregg (1944) have adequately treated these associations, the latter two in correlation with the ant fauna.

All nests collected were immediately placed in bags and taken to the laboratory for separation from the soil. Population counts were kept and the data obtained for individual nests (Table II) confirmed the field observations that *americanus* has the more populous colonies. Cole (1940) reports the same observations in the Great Smoky Mountains. Where nests were collected from clay soil or logs, a Berlese funnel (with copper mesh near the top on which to place the soil and with the stem leading into an alcohol vial) was used for separating out the workers. A goose neck reading lamp placed above the funnel facilitated drying the soil, and with increasing desiccation the ants retreated into the funnel and dropped into the vial. This technique was very useful for all the *americanus* collections in soil and in logs and for the *neoniger* from clay soil. However, since most *neoniger* collections were made in sand, and since a copper mesh large enough to allow the workers to pass would not hold back the sand, the Forel arena (an area surrounded by dry plaster of Paris) was found most satisfactory for separating this ant. A goose neck lamp was again placed above the sand to hasten drying and a nest containing a moist sponge served as the retreat. When the ants had moved into the nest, they were anaesthetized and preserved. In both species some deaths undoubtedly occurred in transit from the field, particularly in nests collected in sand, and in all cases the entire population was not secured, for foraging workers were always missed.

ECOLOGY OF *LASIUS NEONIGER* EMERY AND *LASIUS AMERICANUS*
EMERY IN THE CHICAGO REGION

Lasius neoniger nests were usually in the soil and surmounted by a small crater. Out of forty-one collection records (Table II) only two exceptions occurred: one was in a log and the other was in both log and soil. The species was common in the early stages of dune succession on sand. Its numerous craters were characteristic of the fore and poplar dunes and were found about hummocks containing sand cherry or the sand grasses. In the pine dunes some humus has been added to the sand and the forest cover cuts down the temperature and humidity ranges, but *neoniger* craters continue to be abundant in the clearings. In the black oak dunes its nests are plentiful but they are usually restricted to the more open barren sand. When the mesic red-white oak stage is reached with its well covered forest floor and thick layer of humus, *neoniger* is rarely found. Two collections were made in this associates: one, at Tremont, Indiana, was about a grass root in a roadbed leading into the woods; the other was at Ogden Dunes, Indiana, in a clearing within the forest. A colony was found also in the beech-maple forest at Lakeside, Michigan, but again in a clearing, not in the forest proper. In the flood plain forest adjoining Coffee Creek near Chester-ton, Indiana, specimens of *neoniger* were obtained at the upper margin of the forest where the soil was drier and the cover less dense. Four soil collections in clay pasture were made, three at New Lenox, Illinois, of which two were beneath stones, and one at Volo, Illinois.

Thus *Lasius neoniger* is common in the foredune, poplar, pine, and black oak dunes, and in the last of these it is restricted to the more open areas with little ground cover. It also is frequently found on clay pasture. Thirty-seven of the forty-one *neoniger* collections (Table II) were from these associations and the remaining four made in more mesic habitats were always in open, drier areas within the forests. It is relevant to recall the reference to Talbot that *neoniger* is among the ants able to live on clay but more abundant on sand and apparently limited in distribution by lack of an open substratum.

Collecting of *Lasius neoniger* was difficult. First, the nests were largely in sand which readily collapses. Second, colonies were dug using a long handled deep spade and many times not a worker would be unearthed, a queen never was found, and brood only four times in forty-one worker collections. It had been noted repeatedly that craters were usually clustered within a radius of a few feet. In an effort to determine whether these craters were individual or multiple nests, one about four inches in diameter, an inch high, nine feet from the nearest *Lasius* mound and not associated with any vegetation, was chosen. A trench eighteen inches deep was dug completely around it with a radius of two feet from the nest entrance. A dry sand mulch about two inches in depth was present below which the sand was moist and firm enough to trace ant tunnels. Starting from one side the sand was sliced away and five horizontal galleries were found to spread star-like from a depth of two and one-half inches below the crater mouth. No sign of nest chambers, workers or brood was seen, though the crater had obviously been recently worked. Whether the passages connected with other entrances or whether four feet was not a large enough diam-

eter to avoid destruction of the brood chambers in making the original trench, is not known.

This information on nest size and number of craters in *Lasius neoniger* can be compared with work done on *americanus* by Gaige (1914), Headley (1941), and Forbes (1908). Gaige reports numerous colonies of *americanus* along the sandy beaches on the largest of the Charity Islands. Sometimes small craters were constructed one to six inches in diameter, and one quarter to two inches high, with an opening at the bottom of the cup. He found that the burrows led straight down for an inch or two before turning, the looseness of the sand preventing further observation. Also a swarm of males was noticed from one crater only, though there were probably fifty colonies in a thirty foot circle, which at the time of the swarm were abnormally quiet. He believes this fact may indicate all the craters were "offshoots of the same parent nest and were so closely associated that the males made their exit by the same passages." In Ohio, Headley attempted to determine whether a cluster of *americanus* anthills represented one colony or several and, if several, the extent of each. Foraging territories and odor trails plus data obtained by digging one nest, failed to answer the problem conclusively. Forbes using nest odor recognition, determined the number of craters to a nest of *americanus* in two plots of a cornfield.

Table II shows the distribution of *americanus* in the Chicago region. Twenty-nine of the forty collections were in log decay stages two through five (Talbot) and one collection was in soil and log. Nests of this species may also occur in the soil, in which case small craters are formed if the nest is not under a rock or log, and the remaining ten collections were nests in earth. Of these ten, four were in soil beneath rocks.

Lasius americanus is found in the more mesic collecting sites in the area. This ant does not occur in the dune succession until the black oak stage, and is present in the deeper forest in contrast to *Lasius neoniger* which is found in the open clearings. *Americanus* is common in the mixed oak forest and is one of the most abundant ants in the climax beech-maple forests of the region. It is frequent in the flood plain forest proper at Coffee Creek, and has been collected in the senescent tamarack bog and in the prairie on sand at Dune Acres, Indiana. The form has also been taken in clay pasture at New Lenox and Palos Park, Illinois, and of the three *americanus* records from this habitat, two were nesting under stones and a third was both in the soil and the log covering it. In distribution the two species overlap in pasture on clay.

STATISTICAL STUDY: APPARATUS, TECHNIQUE, RESULTS

The taxonomic difference between the workers of the two species is the presence of erect hairs on the scape of the antenna and the tibiae of *neoniger* and their absence in *americanus*. The hairs on the scape of the antennae and on all segments of the six legs of twenty specimens of each of the varieties were counted to determine statistically the validity of the taxonomic status of the two forms. Twenty was arbitrarily chosen as a preliminary number, and since the differences proved

TABLE III
Comparison of Hairiness of Podomeres of *Lasius neoniger* Emery With *Lasius americanus* Emery
L. N. = *Lasius neoniger* L. A. = *Lasius americanus*

Right or Left	Appendages	<i>Lasius neoniger</i> N = 20				<i>Lasius americanus</i> N = 20				Comparison of M _{L.N.} with M _{L.A.}	
		No. of Hairs	M	S. D.	V	No. of Hairs	M	S. D.	V	S.E. of Mean Difference (M _{L.N.} - M _{L.A.})	$\frac{M_{L.N.} - M_{L.A.}}{S.E. M_{L.N.} - M_{L.A.}}$
R1 L1 R2 L2 R3 L3	Coxae	395	19.75±0.833	3.726	18.866	207	10.35±0.432	1.930	18.647	0.938	10.018
	Coxae	396	19.8±0.612	2.737	13.823	208	10.4±0.497	2.223	21.375	0.788	11.924
	Coxae	360	18.0±0.608	2.720	15.111	160	8.0±0.274	1.225	15.312	0.667	14.993
	Coxae	378	18.9±0.650	2.948	15.598	164	8.2±0.344	1.536	18.732	0.743	14.395
	Coxae	335	16.75±0.591	2.643	15.779	131	6.55±0.250	1.117	17.053	0.642	15.895
R1 L1 R2 L2 R3 L3	Coxae	325	16.25±0.509	2.278	14.018	127	6.35±0.267	1.195	18.819	0.610	16.231
	Trochanters	115	5.75±0.390	1.299	22.591	42	2.1±0.156	0.7	33.333	0.330	11.061
	Trochanters	118	5.9±0.367	1.640	27.797	49	2.45±0.150	0.660	27.306	0.306	8.711
	Trochanters	100	5.0±0.283	1.265	25.3	55	2.75±0.120	0.536	19.491	0.307	7.324
	Trochanters	101	5.05±0.328	1.465	29.01	54	2.7±0.124	0.557	20.630	0.350	6.704
R1 L1 R2 L2 R3 L3	Trochanters	104	5.2±0.288	1.288	24.769	43	2.15±0.107	0.477	22.186	0.307	9.928
	Trochanters	102	5.1±0.199	0.889	17.431	45	2.25±0.120	0.536	23.822	0.232	12.278
	Femora	802	40.1±1.769	7.911	19.728	90	4.5±0.350	1.565	34.778	1.803	19.741
	Femora	787	39.35±1.952	8.731	22.188	89	4.45±0.328	1.465	32.921	1.980	17.630
	Femora	643	32.15±2.075	9.280	28.865	56	2.8±0.207	0.927	33.107	2.086	14.073
R1 L1 R2 L2 R3 L3	Femora	689	33.45±2.211	9.887	29.558	57	2.85±0.215	0.963	33.790	2.221	13.776
	Femora	502	25.1±1.598	7.148	28.478	30	1.5±0.166	0.742	49.467	1.607	14.686
	Femora	466	23.3±1.668	7.457	32.004	33	1.65±0.146	0.654	39.636	1.674	12.934
	Tibiae	256	11.3±1.321	5.908	52.283	0					
	Tibiae	238	11.9±1.172	5.243	44.059	0					
R1 L1 R2 L2 R3 L3	Tibiae	375	18.75±1.775	7.936	42.325	0					
	Tibiae	404	20.2±1.727	7.724	38.238	0					
	Tibiae	380	19.0±1.589	7.106	37.4	0					
	Tibiae	382	19.1±1.665	7.446	38.984	0					
R L	Scapes	422	21.1±1.906	8.526	40.408	0					
	Scapes	419	20.95±1.715	7.671	36.616	0					

significant it was not increased. The specimens of each form were selected from ten different collections and represent the ecological range of these ants. Collections marked by a cross in Table II furnished workers for the study.

The blue daylight glass from the face of the microscope lamp was ideal as a counting background and a hard, smooth surface for manipulating the necessary instruments. The equipment for dissecting the podomeres and for holding them in place under the microscope was simple. Two watch-maker's forceps ground to a very fine point plus needles made by fusing minuten insect pins to glass rod handles proved sufficient.

Technical problems were twofold. The first concerns separation of the podomeres and their firm fixation in the field of vision with freedom to rotate them and see the hairs on all sides. The needles were used to separate the podomeres while the forceps held the body of the ant securely. The trochanter was found most easily manipulated if left attached to the coxa. For counting, the parts were held firmly against the blue glass by means of the forceps and rotated, or raised and lowered for depth.

The second problem involved reaching an arbitrary distinction between hairs, raised pubescence, and bristles (a few bristles were usually present at the ends of the appendage segments and the scape). After considerable experimentation, the following distinction was found to hold and was adhered to throughout. When doubt existed as to the nature of the integumentary outgrowth, a drop of alcohol was placed on the podomere. Bristles were found to remain upright under this treatment. Pubescence and hairs both clung to the chitin while the alcohol was present but the moment it evaporated the hairs rose again from the surface. If a suspected hair remained affixed to the integument, it was considered pubescence and was not counted. Likewise, if an outgrowth remained upright it was regarded as a bristle. In many cases in the more pilose *neoniger*, it was necessary to count the hairs of a given podomere a number of times and to take the mean. The records show a maximum of thirteen and a minimum of four counts made in certain instances. And in all cases in both species every count was made twice.

The statistical results of the work are shown in Table III. In comparing the difference of the means divided by its standard error for each podomere of *Lasius neoniger* and *Lasius americanus* (e. g. right first coxa—20 specimens of each species), the quotient is greater than two in each instance. This indicates the probability is less than five in a hundred of the results being obtained by chance and is therefore considered significant.

The coefficients of variation (Table III) were computed for the podomeres ($N=20$), and the standard errors of the difference between them were calculated, (1) between the species for the same podomere, and (2) within the species in terms of podomeres. When the differences between podomere variation coefficients were divided by their standard errors, the following conclusions were drawn. Comparing the species, only the differences between the right first and the right third femora are significant (quotient greater than 2). Within a species *Lasius*

neoniger and *Lasius americanus* demonstrate: (1) no consistent significant differences within a podomere from the anterior to the posterior end of the body; (2) no significance within a podomere between the right and left sides of the body; (3) within an appendage, significances are sporadic though with two exceptions (and one of these a border line case) the differences between coxa and femur are always significant.

TABLE IV

Comparison of Coefficients of Variation of *Lasius neoniger* Emery with *Lasius americanus* Emery When Podomeres Grouped (N=120).

L. N. = *Lasius neoniger*

L. A. = *Lasius americanus*

Podomeres	<i>Lasius neoniger</i>				<i>Lasius americanus</i>				Comparison of V _{L.N.} with V _{L.A.}	
	No. of Hairs	M	S.D.	V	No. of Hairs	M	S.D.	V	S.E. of V Difference (V _{L.N.} -V _{L.A.})	V _{L.N.} -V _{L.A.} S.E. V _{L.N.} -V _{L.A.}
Coxae.....	2189	18.242±0.291	3.191	17.493	997	8.308±0.207	2.265	27.262	2.091	4.772
Trochanters...	640	5.333±0.126	1.374	25.771	288	2.4 ±0.058	0.638	26.571	2.074	0.386
Femora.....	3869	32.242±0.968	10.6	32.875	355	2.958±0.148	1.625	54.928	4.132	5.337
Tibiae.....	2005	16.708±0.718	7.861	47.047	0					

TABLE V

Comparison Within a Species of Coefficients of Variation of the Grouped Leg Podomeres (N=120).

PODOMERES	<i>Lasius neoniger</i>		<i>Lasius americanus</i>	
	S.E. of V Difference	V Difference	S.E. of V Difference	V Difference
		S.E. of V Difference		S.E. of V Difference
Coxae with Trochanters....	1.623	5.099	2.457	0.281
Trochanters with femora....	2.422	2.934	3.939	7.2
Coxae with femora.....	2.404	6.399	3.958	6.989
Coxae with tibiae.....	3.24	9.122		
Trochanters with tibiae....	3.253	6.540		
Femora with tibiae.....	3.705	3.825		

The leg podomeres were then grouped (N=120). Again the coefficients of variation, the standard errors of their differences, and the variation coefficient differences divided by their standard errors were computed between and within the species. Between the species for the same podomere (Table IV), the differences between the coxae and femora are significant. Within a species between podomeres (Table V), all the differences proved significant except between the *americanus* coxae and trochanters.

These data on the grouped podomeres are interesting in that they indicate an increase in relative variability in terms of pilosity from the proximal to the distal end of a given appendage in these two species. *Americanus* does not illustrate the increase in the proximal podomeres but between these and the femora, the increase is highly significant.

Also, the data demonstrate that *americanus* is relatively the more variable of the two species in leg pilosity. The coefficients of variation of the grouped data are shown graphically in figure 1 for the two species.

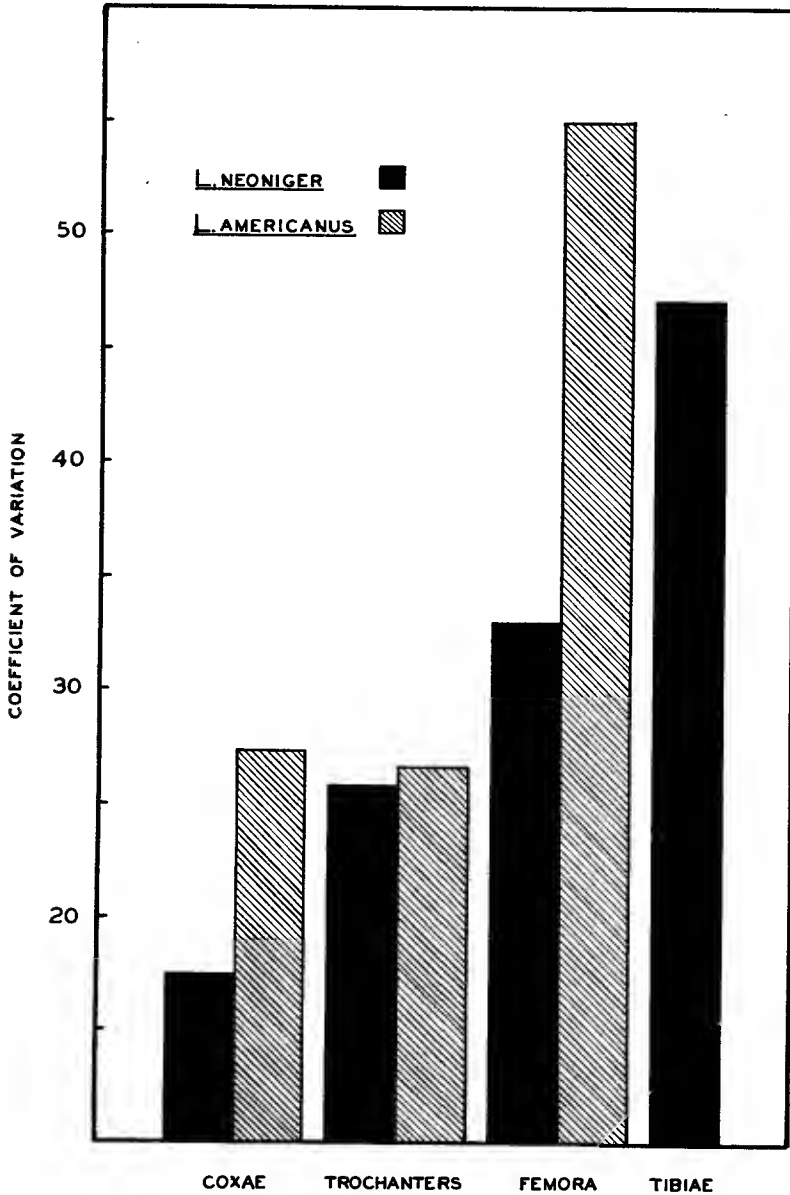


FIG. 1. Bar diagram of the coefficients of variation for the grouped leg podomeres (N=120) of the two species.

DISCUSSION

Thus as seen in Table III, the taxonomic criterion used to separate the workers of the two forms is valid statistically. Furthermore, as shown in figure 2, there were no cases of overlap in appendage and scape hairiness between them. A bimodal curve develops when hair number of both forms is plotted against the number of individuals involved. Interestingly, the four lowest of the twenty *neoniger* counts (250-350 hairs) are from only two of the ten colonies used. *Neoniger* has a greater spread than *americanus*. If the scape and tibial hair is

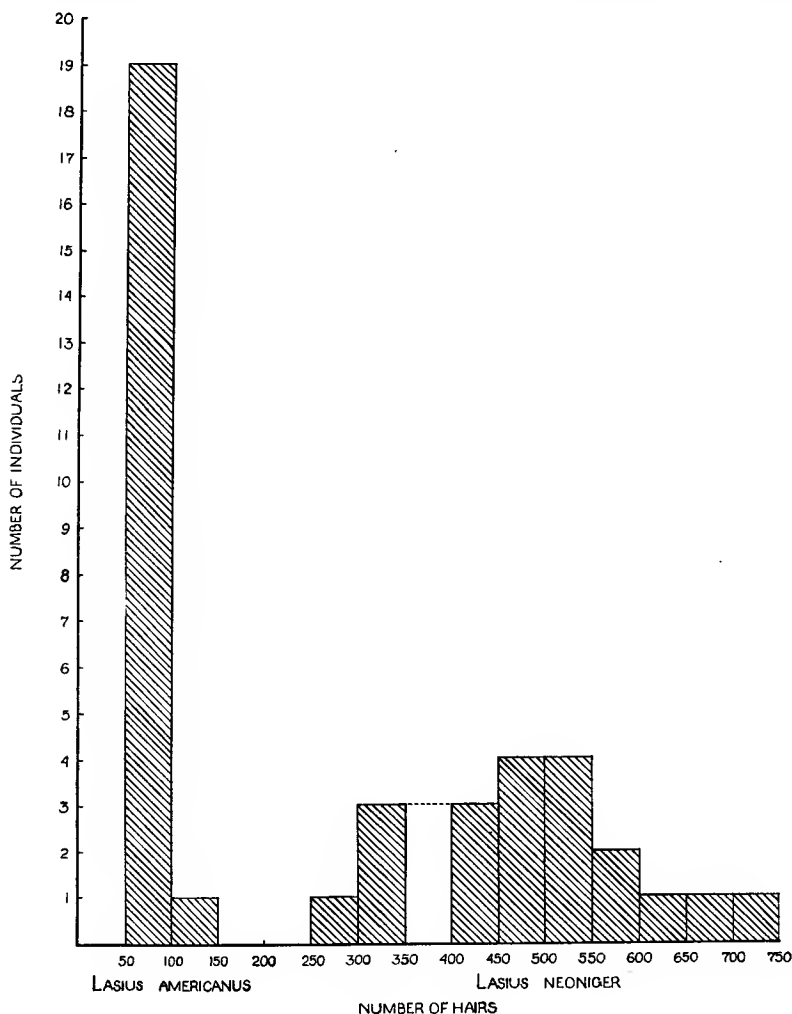


FIG. 2. Graph showing bimodality when the scape and leg hairiness of the workers of *Lasius americanus* Emery is compared to that of the workers of *Lasius neoniger* Emery. Twenty individuals of each variety are represented.

excluded from the *neoniger* pilosity counts, the resulting *neoniger* histogram shows less spread (from 200–450 hairs) but remains distinct from *americanus*. On the basis of this clear separation, it is advisable to consider these forms as non-intergrading populations and therefore distinct species to be called *Lasius neoniger* Emery and *Lasius americanus* Emery. It should be pointed out, however, that species may be distinct even with overlapping characters (e. g., Emerson 1935; Dobzhansky and Epling 1944). These taxonomic distinctions are correlated with the ecology of the two forms. Comparing their distribution in the Chicago region as demonstrated in Table II, the lack of extensive mingling is readily seen. The ecological differences are discussed fully in an earlier section.

A species is an evolved or evolving, genetically distinctive, reproductively isolated, natural population (Emerson 1945). *Lasius neoniger* and *americanus* conform to this species concept though just what factors are isolating these populations are not fully known. The isolating phenomena (Emerson 1943) are obviously not geographic but apparently are partially ecologic with the forms overlapping only in pasture on clay. The species swarm annually and over the same seasonal period (Table I). Diurnal variation in swarming time is doubtful. The author observed numerous *neoniger* swarms in the Chicago region which always took place in the early evening. There were only two accounts found in the literature on the swarming hour. A record for *americanus* was given as taking place "a little before dark" (Gauge 1914). Turner (1915) described a swarming flight of *Lasius niger* (probably *neoniger* though variety not indicated—see earlier hybridization discussion); observations began about three o'clock in the afternoon and the pre-nuptial activities and mating continued "until about the close of day."³ Sexual isolation might be involved either through behavioristic, mechanical, or physiological incompatibilities, but no information is available. Wright (1940) states that geographic and ecologic isolation which promote slow accumulation of genetic differences usually precedes interspecific sterility and the species under study may be a case in the process of reaching largely complete cross-sterility.

It appears profitable on the basis of the present study to make a similar analysis of the differences between the Palearctic forms. Diver (1940), working in the South Haven Peninsula, England, found differences in distribution of *Lasius niger* and *Lasius alienus* which are the reverse of the Nearctic forms reported in the present paper. Also, with the availability of adequate series from the entire Nearctic region, an intensive revision of the *niger* group would be exceedingly valuable. The differences in queen size in *Lasius americanus* (Wheeler 1917) and in *Lasius neoniger* (Wheeler 1908, 1917) indicate there are very likely more forms in North America than at present recognized.

SUMMARY

1. On the basis of the non-intergrading character of scape and leg hairiness, the varieties *Lasius niger* (L.) var. *neoniger* Emery and

³Talbot (1945) records *Lasius americanus* swarming between 3:30 and 6:00 P. M. (Central Standard Time), in her yard at Tiffin, Ohio.

Lasius niger (L.) subsp. *alienus* Förster var. *americanus* Emery are raised to specific rank, namely, *Lasius neoniger* Emery and *Lasius americanus* Emery. Their ecological differences substantiate the elevation.

2. When the morphological difference between these forms was tested statistically, no cases of overlap between them were noted.

3. Collections of *neoniger* and *americanus* were made in the major habitats of the Chicago area.

4. *Lasius neoniger* was common in the early dune succession stages and *americanus* prevailed in the more mesic associates. Both are present in clay pasture land. Where the forms mingle in forest communities, they do not occur in ecologically equivalent situations. An open substratum on sand seems to favor *neoniger*.

5. Forms occur in both soil and logs but *neoniger* is usually a soil, and *americanus* a log inhabitant.

6. Populations of *americanus* colonies appear larger than those of *neoniger*.

7. *Americanus* demonstrates greater relative variability in leg pilosity than does *neoniger*.

8. A statistically significant increase in relative variability in terms of pilosity is shown in these two species from the proximal to the distal end of a given appendage.

LITERATURE CITED

- Amstutz, M. E. 1943. The ants of the Kildeer Plain Area of Ohio. *Ohio Jour. Sci.* 43: 165-173.
- Bondroit, J. 1918. Les fourmis de France et de Belgique. *Ann. Soc. Ent. France* 87: 1-174.
- Buren, W. F. 1944. A list of Iowa ants. *Iowa State Coll. Jour. Sci.* 18: 277-312.
- Burrill, A. C., and M. R. Smith. 1919. A key to the species of Wisconsin ants, with notes on their habits. *Ohio Jour. Sci.*, 19: 279-292.
- Cole, A. C., Jr. 1933. Ant communities of a section of the sagebrush semi-desert in Idaho, with special reference to the vegetation. *Ent. News* 44: 16-19.
1934. An annotated list of the ants of the Snake River Plains, Idaho. *Psyche* 41: 221-227.
1938. Suggestions concerning taxonomic nomenclature of the hymenopterous family Formicidae, and descriptions of three new ants. *Amer. Midl. Nat.* 19: 236-241.
1940. A guide to the ants of the Great Smoky Mountains National Park, Tennessee. *Amer. Midl. Nat.* 24: 1-88.
1942. The ants of Utah. *Amer. Midl. Nat.* 28: 358-388.
- Cowles, H. C. 1901. The plant societies of Chicago and vicinity. *Geog. Soc. of Chicago, Bull. No. 2*, 76 pp.
- Creighton, W. S. 1938. On Formicid nomenclature. *Jour. New York Ent. Soc.* 46: 1-9.
- Davis, W. T., and J. Bequaert. 1922. An annotated list of the ants of Staten Island and Long Island, New York. *Bull. Brooklyn Ent. Soc.* 17: 1-25.
- Dennis, C. A. 1938. The distribution of ant species in Tennessee with reference to ecological factors. *Ann. Ent. Soc. Amer.*, 31: 267-308.
- × Diver, C. 1940. The problem of closely related species living in the same area. In: Huxley, J., *The New Systematics*: 303-328.
- Dobzhansky, Th. and C. Epling. 1944. Contributions to the genetics, taxonomy, and ecology of *Drosophila pseudoobscura* and its relatives. *Carn. Inst. Wash. Pub.* 554.

- Donisthorpe, H. 1915. British ants, their life history and classification. Plymouth, 379 pp.
1927. British ants, their life history and classification. London, 436 pp., 2nd Ed.
- Emerson, A. E. 1935. Termitophile distribution and quantitative characters as indicators of physiological speciation in British Guiana termites (Isoptera). Ann. Ent. Soc. Amer. 28: 369-395.
1943. Ecology, evolution and society. Amer. Nat. 77: 97-108.
1945. Taxonomic categories and population genetics. Ent. News 56: 14-19.
- Emery, C. 1893. Beiträge zur Kenntnis der Nordamerikanischen Ameisenfauna. Zool. Jahrb. Syst. 7: 633-682.
- Forbes, S. A. 1908. Habits and behavior of the cornfield ant, *Lasius niger americanus*. Univ. Ill. Agr. Exp. Sta. Bull. No. 131: 29-45.
- Förster, A. 1850. Hymenopterologische Studien. Aachen, ter Meer 1: 74 pp.
- Fuller, G. D. 1925. The vegetation of the Chicago region. Univ. Chicago Press, pp. 1-27.
- Gaige, F. M. 1914. Results of the Mershon Expedition to the Charity Islands, Lake Huron. The Formicidae of Charity Island. Occ. Pap. Mus. Zool., Univ. Michigan No. 5: 1-29.
- Gregg, R. E. 1944. The ants of the Chicago region. Ann. Ent. Soc. Amer. 37: 447-480.
- Hayes, W. P. 1925. A preliminary list of the ants of Kansas. Ent. News 36: 10-12, 39-43, 69-73.
- Headley, A. E. 1941. A study of nest and nesting habits of the ant *Lasius niger* subsp. *alienus* var. *americanus* Emery. Ann. Ent. Soc. Amer. 34: 649-657.
1943. The ants of Ashtabula County, Ohio. Ohio Jour. Sci. 43: 22-31.
- Mallis, A. 1941. A list of the ants of California with notes on their habits and distribution. Bull. So. Calif. Acad. Sci. 40: 61-100.
- Mayr, E. 1942. Systematics and the Origin of Species. Columbia Univ. Press, 334 pp.
- Mayr, G. 1886. Die Formiciden der Vereinigten Staaten von Nordamerika. Verhandlungen d. Zoologisch-Botanischen Gesellschaft in Wien 36: 419-464.
- Morris, R. L. 1943. An annotated list of the ants of Indiana. Proc. Indiana Acad. Sci. 52: 203-224.
- Provancher, L'Abbé. 1881. Faune Canadienne. Deuxième Division des Hyménoptères. Family X. Formicidae. Le Naturaliste Canadien 12 (143): 321-333; (144): 353-362.
1887. Additions et corrections an Volume II de la Faune Entomologique de Canada. Traitant des Hyménoptères. 475 pp. Les Formicids pp. 224-249.
- Rau, P. 1934. Behavior notes on certain ants of St. Louis County, Missouri. Trans. Acad. Sci. St. Louis 28: 207-215.
- Smith, M. R. 1927. An additional annotated list of ants of Mississippi, with a description of a new species of *Pheidole*. Ent. News 38: 308-314.
- 1934a. A list of the ants of South Carolina. Jour. New York Ent. Soc. 42: 353-361.
- 1934b. Dates on which the immature or mature sexual phases of ants have been observed. Ent. News 45: 247-251, 264-267.
- Sturtevant, A. H. 1931. Ants collected on Cape Cod, Massachusetts. Psyche 38: 73-79.
- Talbot, M. 1934. Distribution of ant species in the Chicago region with reference to ecological factors and physiological toleration. Ecol. 15: 416-439.
1945. A comparison of flights of four species of ants. Amer. Midl. Nat. 34: 504-510.
- Tanquary, M. C. 1913. Biological and embryological studies on the Formicidae. Part I. The life history of the cornfield ant, *Lasius niger* var. *americanus* Emery. Bull. Ill. State Lab. Nat. Hist. 9: 417-443.
- Turner, C. H. 1915. The mating of *Lasius niger* L. Jour. Anim. Behav. 5: 337-340.
- Wesson, L. G., Jr., and R. G. Wesson. 1940. A collection of ants from south central Ohio. Amer. Midl. Nat. 24: 89-103.
- Wheeler, W. M. 1904. The ants of North Carolina. Bull. Amer. Mus. Nat. Hist. 20: 299-306.
1905. An annotated list of the ants of New Jersey. Bull. Amer. Mus. Nat. Hist. 21: 371-403.

- Wheeler, W. M.** 1908. The ants of Casco Bay, Maine, with observations on two races of *Formica sanguinea* Latreille. *Bull. Amer. Mus. Nat. Hist.* 24: 619-645.
1910. Colonies of ants (*Lasius neoniger* Emery) infested with *Laboulbenia formicarum* Thaxter. *Psyche* 17: 83-86.
- 1916a. A list of Indiana ants. *Proc. Indiana Acad. Sci.*, pp. 460-466.
- 1916b. Hymenoptera of Connecticut. Formicoidea. *Connect. Nat. Hist. Surv., Bull.* 22: 577-601.
1917. The mountain ants of western North America. *Proc. Amer. Acad. Arts Sci.* 52: 457-569.
- Wright, S.** 1940. The statistical consequences of Mendelian heredity in relation to speciation. In: Huxley, J., *The New Systematics*: 161-183.